

SYSTEMATICS OF *PSEUDOCLOEON*, *ACENTRELLA*,
BAETIELLA, AND *LIEBEBIELLA*, NEW GENUS
(EPHEMEROPTERA: BAETIDAE)

R. D. WALTZ¹ AND W. P. MCCAFFERTY

Department of Entomology, Purdue University, West Lafayette, Indiana 47907

Abstract.—Detailed character analysis has allowed a more natural classification in the Baetidae as follows. *Pseudocloeon* Klapálek must presently be restricted to the type species, *P. kraepelini* Klapálek, a species known only from adults. Certain *Pseudocloeon* species are placed in the genera treated here. *Liebebiella*, new genus, includes: *L. orientale* (Müller-Liebenau), new combination (type species); *L. ambigua* (Müller-Liebenau), new combination; *L. atoki* (Müller-Liebenau), new combination; *Liebebiella deigma*, n. sp.; *L. difficila* (Müller-Liebenau); *L. klapaleki* (Müller-Liebenau), new combination; *L. proxima* (Müller-Liebenau), new combination; *L. siveci* (Braasch), new combination; and *L. vera* (Müller-Liebenau), new combination. *Acentrella* Bengtsson is revised to include: *A. lapponica* Bengtsson (type species); *A. ampla* Traver; *A. carolina* (Banks), new combination; *A. chantauensis* (Kluge), new combination; *A. fenestrata* (Kazlauskas), new combination; *A. gnom* (Kluge), new combination (= *Pseudocloeon ultimum* Müller-Liebenau, new synonymy); *A. insignificans* (McDunnough), new combination; *A. lata* (Müller-Liebenau), new combination; *A. sibirica* (Kazlauskas), new combination; *A. sinaica* Bogoescu; *A. tonneri* (Braasch and Soldán), new combination; and *A. turbida* (McDunnough), new combination. *Baetiella* Ueno (= *Neobaetiella* Müller-Liebenau, new synonymy) is revised and includes: *B. japonica* (Imanishi) (type species); *B. aino* (Matsumura), new combination; *B. armata* Braasch; *B. ausobskyi* Braasch; *B. bispinosa* (Gose), new combination (= *Neobaetiella macani* Müller-Liebenau, new synonymy); *B. imanishii* Braasch; *B. innotata* (Braasch), new combination; *B. ladakae* Traver; *B. marginata* Braasch; *B. muchei* (Braasch), new combination; *B. tuberculata* (Kazlauskas), new combination; and *B. ursina* (Kazlauskas), new combination. *Neobaetiella imanishi* Müller-Liebenau is a nomen nudum, and *Neobaetiella uenoi* Müller-Liebenau is an unavailable name.

Baetid mayflies classified in the genera *Acentrella* Bengtsson, *Baetiella* Ueno, *Barbaetis* Waltz and McCafferty, *Heterocloeon* McDunnough, *Platybaetis* Müller-Liebenau, as well as most Holarctic *Baetis* Leach (Waltz and McCafferty, 1987a) and *Pseudocloeon* Klapálek sensu auctt. are distinguished from the larvae of all other baetids by their synapomorphic possession of a ventral femoral patch (Figs. 1, 4, 5, 12, 17). Within this grouping, which we call the *Baetis* complex of genera, generic classification has been dubious and polyphyletic, at least in part, because of the historical use of phylogenetically unreliable adult characters as *prima facie* generic criteria. In particular, the number of forewing marginal intercalaries and the relative size and venational characters of the hindwings have been emphasized. Our extensive morphological study of the *Baetis* complex of genera indicates that such wing characters do not necessarily reflect phyletic relationships. The reduction of the hindwing and its venation, although apomorphic, cannot be used alone for deciphering generic relationships because they are highly subject to parallel evolution and often accompany the widespread and independent reductionistic tendencies found among many different lineages of baetids.

¹ Current address: Thames Science Center, Gallows Lane, New London, Connecticut 06320.

Recent studies of *Baetis*, e.g., Müller-Liebenau (1970, 1973a) and Morihara and McCafferty (1979a, b), have elucidated numerous larval characters of systematic use for *Baetis* species that are also generally applicable to other genera of the *Baetis* complex but not to all Baetidae. Species-level systematics of Baetidae is now primarily based on larval morphology (Müller-Liebenau, 1981; Müller-Liebenau and Hubbard, 1986) but, to a large degree, generic limits have remained adult oriented. Our incorporation of cladistically informative larval characterization for defining generic limits has led to the revisionary systematics of the *Baetis* complex genera *Pseudocloeon*, *Acentrella*, and *Baetiella*, and the description of a new genus.

Institutions and individuals that loaned material for this study and the acronyms by which they are cited are B. Kondratieff (BK), Cornell University (CU), Harvard Museum of Comparative Zoology (MCZ), Oregon State University (OrSU), Purdue Entomological Research Collection (PERC), Stroud Water Research Center (SWRC), National Museum of Natural History, Washington, D.C. (USNM), University of Utah (UU), Virginia Polytechnic Institute and State University (VPI), and the Zoologisches Staatsmuseum, Munich (ZSM).

Pseudocloeon Klapálek, 1905

Description. Larva. Unknown. Adult. The adult was recently redescribed by Waltz and McCafferty (1985a).

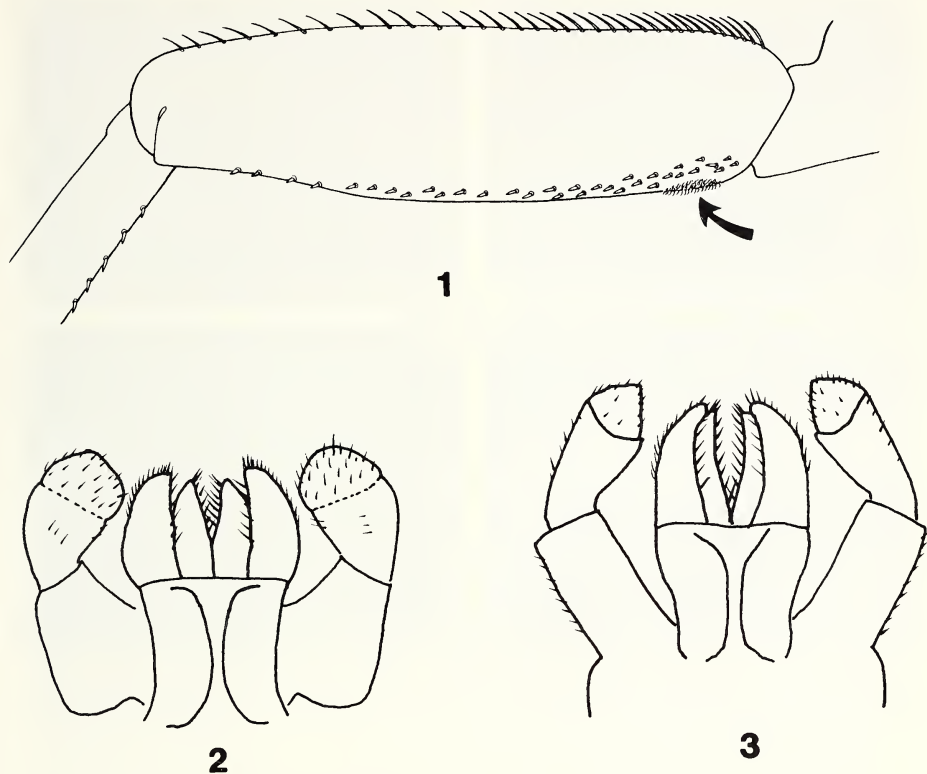
Type species. *Pseudocloeon kraepelini* Klapálek 1905:105, by monotypy.

Material examined. Lectotype, male imago, Java, Buitenzorg, 24.ii. to 12.iii.1904, leg. P. Kraepelin, des. Waltz and McCafferty, 1985. Paralectotypes, 2 male imagos and 1 subimago, same data as lectotype, des. Waltz and McCafferty, 1985.

Distribution. Java.

Remarks. The only *bona fide* material of the genus *Pseudocloeon* is represented by the type series of four adult specimens deposited at the University of Hamburg. Other adult Baetidae that have been classified as species of *Pseudocloeon* are considered provisionally placed (Müller-Liebenau, 1981) because the genus has been historically characterized solely by the combined characters of paired intercalaries along the forewing margin and the absence of hindwings. Since hindwings have been lost numerous times in many independent lineages of Baetidae (Edmunds et al., 1976; Gillies, 1979; Müller-Liebenau, 1978, 1980, 1981, 1984a; Waltz and McCafferty, 1985b, c, 1986, 1987b, c, d), it follows that not only is there a strong possibility that the group of species presently assigned to *Pseudocloeon* are polyphyletic, but that the type species itself is congeneric with another genus. For example, our review of the type species, *P. kraepelini* (Waltz and McCafferty, 1985a), suggests a close, if not congeneric relationship with some *Baetis* species known in the *Baetis atrebatinus* complex (Müller-Liebenau, 1981, 1984a).

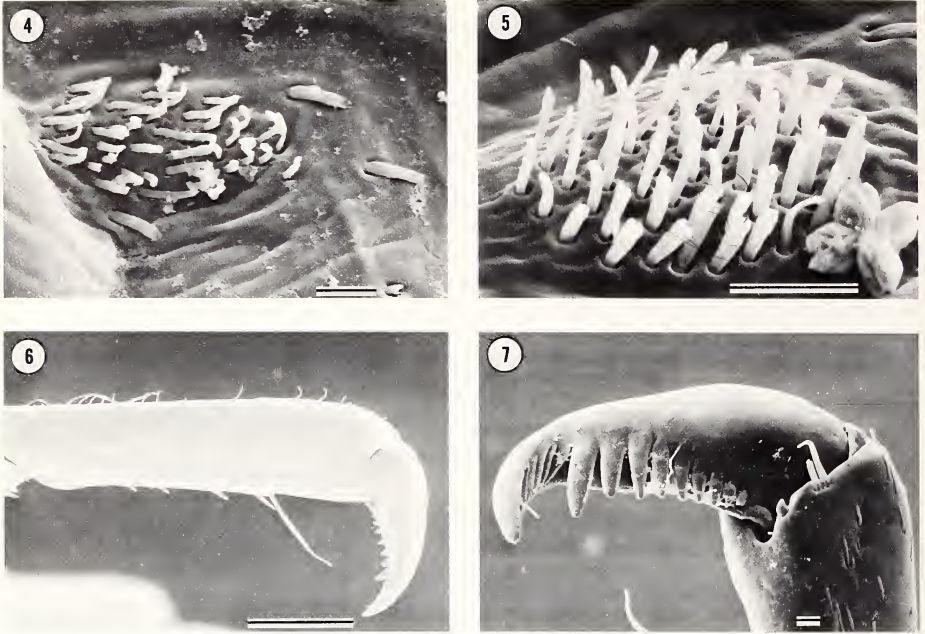
The doubt surrounding the integrity of *Pseudocloeon* would be soluble if the larval stage (the stage necessary for addressing phyletic affinities and taxonomic delimitation in the family Baetidae) of the type species of *Pseudocloeon* were known. Such is not the case and any larvae of species now assigned to *Pseudocloeon* are no more reliably representative of the type species of *Pseudocloeon* than are their associated adults. As the larval stages of the presumed species of *Pseudocloeon* have become known in detail, these species have generally been reclassified into genera with the appropriate



Figs. 1-3. 1. *Acentrella ampla* foreleg showing ventral patch. 2. *Acentrella lapponica* larval labium. 3. *Baetiella japonica* larval labium.

larval affinities (Edmunds, 1974; Edmunds et al., 1976; Müller-Liebenau, 1981; Waltz and McCafferty, 1985b, 1986, 1987b, c). We do not, however, agree with the indiscriminate move of all present *Pseudocloeon* into *Baetis* as per Keffermüller (1980) because there are in fact many included species that will require reassignment to genera other than *Baetis*.

Based on the above we propose that *Pseudocloeon* be restricted at this time to include only the type species from Java, *P. kraepelini*, although we are cognizant that many species will remain by default in *Pseudocloeon* until their larval stages are known and they can be correctly placed to genus. This taxonomic move essentially allows workers to proceed with the necessary revision of the Baetidae without relying on only presumptive concepts of *Pseudocloeon* and also precludes the further proliferation of a nomenclature that most probably would have to be revised at a later date. In keeping with this, we herein transfer many of the Oriental species previously placed in *Pseudocloeon* (Müller-Liebenau, 1981, 1982a, b, 1984b, 1985; Braasch, 1983) to the following new genus in addition to revising the genera *Acentrella* and *Baetiella* to include numerous species previously placed in *Pseudocloeon*.



Figs. 4-7. *Liebebiella* spp. larvae. 4. *L. orientale*, ventral femoral patch. 5. *L. vera*, ventral femoral patch. 6. *L. orientale*, tarsus and claw. 7. *L. orientale*, claw. (Scale: Figs. 4, 5, 7—bar = 10 μ m; Fig. 6—bar = 100 μ m)

Liebebiella, new genus

Description. Larva. Antennae ca. $1.5 \times$ length of head capsule. Mandibular incisors fused (Müller-Liebenau 1982b: figs. 1f, 2d, 3e, 4d, 5d). Maxillary palp two segmented (*ibid.*: figs. 1c, 2c, 3d, 4c, 5c). Labium (*ibid.*: figs. 1b, 2b, 3b, 4b, 5b) with palps shortened (as in Fig. 2); segment 2 of palp with weakly developed inner lobe; segment 3 of palp rounded, weakly tapered, or flattened apically.

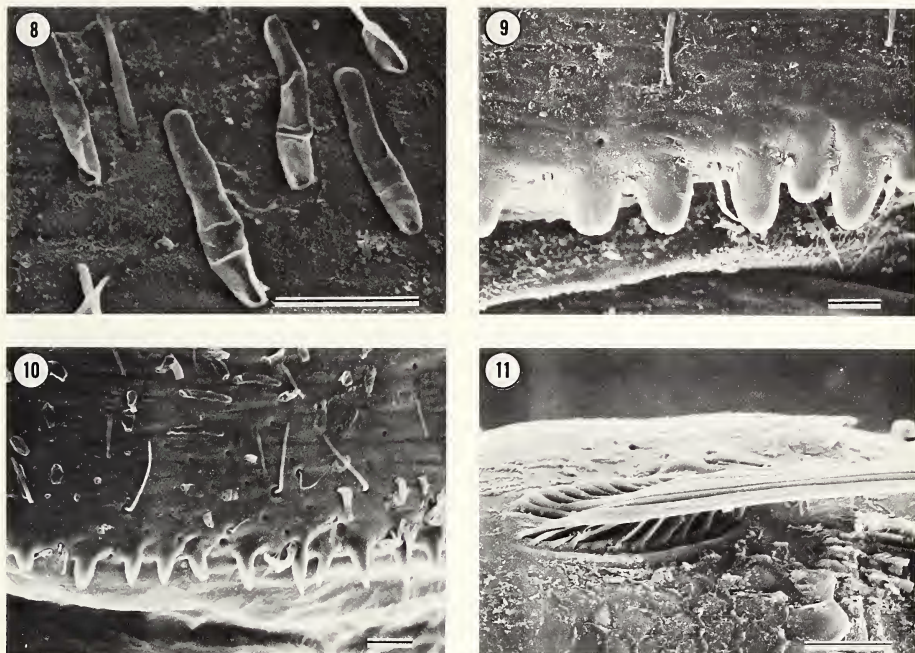
Prothorax with distinctive *lapponica*-type color pattern (*ibid.*: figs. 7, 9, 11) or without such pattern. Femora of all legs with long, multilaterally ciliate bristles (the cilia are relatively long and dense) (Müller-Liebenau, 1981: fig. 4i); ventral femoral patch present (Figs. 1, 4, 5). Metatibia with one or two (*ibid.*: fig. 4i) rows of long ciliate bristles. Tarsus (Fig. 6) of all legs with long, ventral subapical bristle. Claws (Fig. 7) with one row of denticles and one pair of long subapical bristles.

Abdomen without dorsal tubercles; not dorsoventrally flattened. Tergal scales absent, median row of long, hyaline bristles present dorsally; tube scales (Fig. 8) present or absent. Posterior marginal spines (Figs. 9, 10; Müller-Liebenau, 1982b: figs. 8, 10, 12, 13, 14) distinct and entire. Gills simple and without serrate margins. Cerci without (only in the species *L. atoki*) or with (Fig. 11) lateral bristles along interior margin.

Adult. Unknown.

Type species. *Pseudocloeon orientale* Müller-Liebenau, 1982b:289.

Material examined. *Pseudocloeon difficilum* Müller-Liebenau, 3 larvae, FC30/b, 10.xii.1970, We-ganga in Balangopa (Belihuluya), leg. Starmülner, det. Müller-Lie-



Figs. 8–11. *Liebebiella* spp. larvae. 8. *L. vera*, tube scales of abdominal terga. 9. *L. orientale*, tergal posterior margin. 10. *L. vera*, tergal posterior margin. 11. *L. orientale*, cerci. (Scale: Figs. 8–11—bar = 10 μ m)

benau (ZSM). *Pseudocloeon orientale* Müller-Liebenau, 3 larvae, FC23/b, 3.xii.1970, Dickoya River, Maskeliya, leg. Starmülner, det. Müller-Liebenau (ZSM). *Pseudocloeon verum* Müller-Liebenau, 2 larvae, Malaysia, Tributary of the River Gombak, 21 miles N of Uciala Lumpur on Bentong Road, 23.viii.1969, leg. J. E. Bishop, det. Müller-Liebenau (ZSM). *Pseudocloeon* sp. 1 Ulmer, 6 larvae; 5 larvae, FM 7, Tjurup, Musi in Ajer Simpang, 6.v.1929, 1 larva slidemounted (Müller-Liebenau) in euparal(?) and 3 larvae (missing head capsules) in alcohol and 1 male larva with mouthparts, legs, forewing of subimago (extracted from larval wingpads), slidemounted (Müller-Liebenau) in euparal(?), remainder of body in alcohol; 1 male larva, South Sumatra, FM8b, Musi-Gebeit, warm spring Subang Ajam on the Kali Djervih in Tjurup, Mooskaskade, 32°–35°C, 7.v.1929. Prof. Feuerborn, leg slidemounted (Müller-Liebenau) in euparal(?).

Included species. Nominal species of *Liebebiella* (previously Oriental *Pseudocloeon*) include *L. orientale* (Müller-Liebenau), 1982b, **New Combination** (type species); *Liebebiella ambigua* (Müller-Liebenau), 1982b, **New Combination**; *L. atoki* (Müller-Liebenau), 1982a, **New Combination**; *L. difficila* (Müller-Liebenau), 1982b, **New Combination**; *L. klapaleki* (Müller-Liebenau), 1982b, **New Combination**; *L. proxima* (Müller-Liebenau), 1984b, **New Combination**; *L. siveci* (Braasch), 1983, **New Combination**; and *L. vera* (Müller-Liebenau), 1982b, **New Combination**.

We give *Pseudocloeon* sp. 1 of Ulmer (1939) [characterized and illustrated also by

Müller-Liebenau (1981) and diagnostically compared with other species by Müller-Liebenau (1982b)] the formal name *Liebebiella deigma*, n. sp. We designate type specimens of *L. deigma* from Ulmer's original material as follows: Holotype; mature larva, FM 7, Tjurup, Musi in Ajer Simpang, 6.v.1929, slidemounted (Müller-Liebenau) in euparal(?), deposited Zoological Institut and Zoologisches Museum, University Hamburg. Paratypes, 4 larvae, same data as holotype, 3 larvae (missing head capsules) in alcohol, 1 male larva with mouthparts, legs, forewing of subimago (extracted from larval wingpads), slidemounted (Müller-Liebenau) in euparal(?), remainder of body in alcohol; male larva, South Sumatra, FM8b, Musi-Gebeit, warm spring Subang Ajam on the Kali Djervih in Tjurup, Mooskaskade, 32°–35°C, 7.v.1929. Prof. Feuerborn, leg slidemounted (Müller-Liebenau) in euparal(?), deposited Zoological Institut and Zoological Museum, University Hamburg.

Distribution. Oriental.

Etymology. Feminine gender. *Liebebiella*—an arbitrary combination of letters based upon the surname of Ingrid Müller-Liebenau, the German ephemeropterist.

Remarks. The genus *Liebebiella* is distinguished from all other *Baetis* complex genera by the form of its labium (similar to *Acentrella*) along with the combined presence of dorsal femoral bristles that are multilaterally ciliate (the ciliae are relatively long and dense), a greatly elongated distal bristle on the tarsus, and two well-defined rows of metatibial bristles (one row only in the species *L. atoki*).

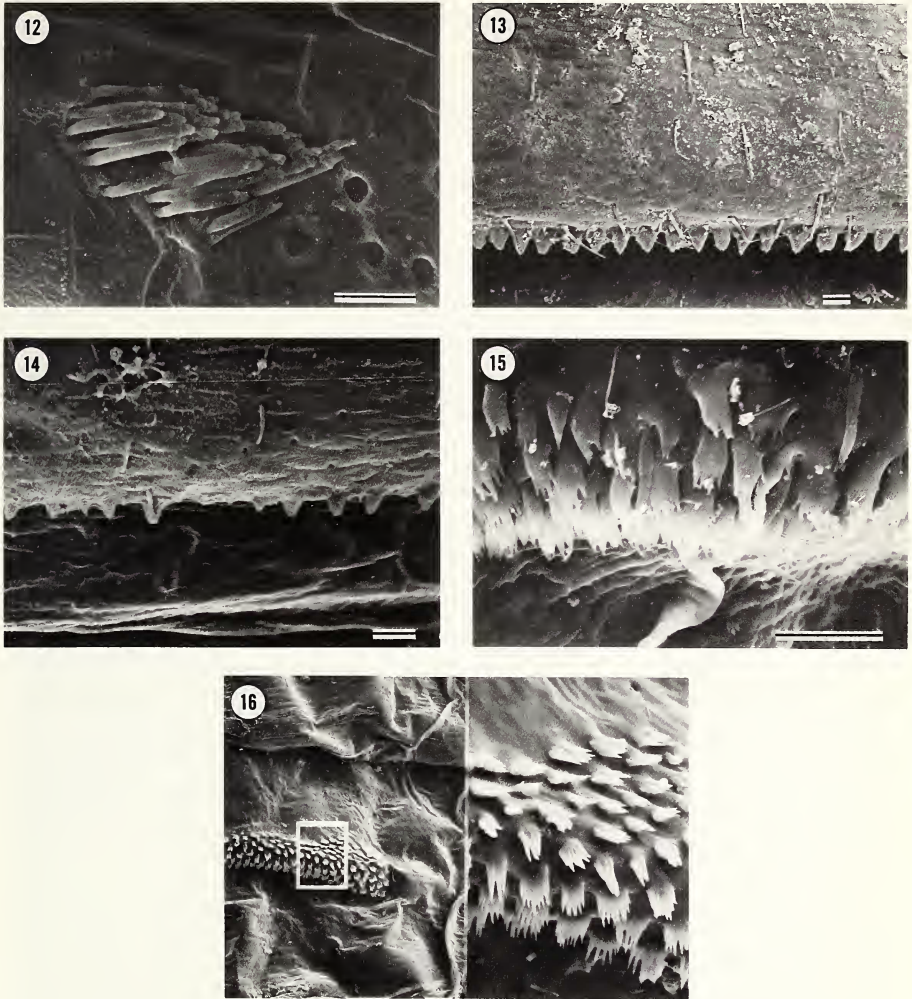
As previously alluded to by Müller-Liebenau (1981, 1982b), the group of species that we have placed in the genus *Liebebiella* is clearly derived from an *Acentrella*-like ancestor possessing all of the apomorphies discussed herein under that genus. In addition, *Liebebiella* possesses a distinctive set of autapomorphic characters, including the presence of multilaterally ciliate (ciliae relatively long and dense) dorsal femoral bristles, two rows of long multilaterally ciliate metatibial bristles (except in *L. atoki*), a long distal tibial bristle, and a distinctive medial row of long hyaline bristles on the abdominal terga [independently derived in other unrelated taxa, e.g., *Baetodes* Needham and Murphy (Cohen and Allen, 1978)].

Acentrella Bengtsson, 1912

Acentrella frequently has been placed in synonymy with the genus *Baetis* (e.g., Edmunds and Traver, 1954; Grandi, 1956, 1960; Müller-Liebenau, 1965, 1970; Edmunds et al., 1976; Morihara and McCafferty, 1979a), or regarded as a subgenus of *Baetis* (e.g., Demoulin, 1970). Most recently it has been recognized as a distinct genus closely allied to Oriental species provisionally assigned to *Pseudocloeon* (Müller-Liebenau, 1981, 1982b).

Description. Larva. Antennae ca. $1.5 \times$ length of head capsule and situated in lower one-third of head capsule (Edmunds et al., 1976: fig. 11). Mandibular incisors completely fused or partially fused (i.e., discernible one from another). Maxillary palp two segmented (Müller-Liebenau, 1970: fig. 46c). Labium (Fig. 2) compact with labial palps (Morihara and McCafferty, 1979a: fig. 13b; Müller-Liebenau, 1970: fig. 46d) reduced; segment 2 of labial palps with weakly developed inner lobe; segment 3 of labial palps evenly rounded to slightly truncate.

Thorax broad and dorsoventrally flattened. Prothorax generally with distinctive *lapponica*-type pattern (Müller-Liebenau, 1970: figs. 43, 44). Femora (*ibid.*: figs. 46c,



Figs. 12–16. *Acentrella* spp. larvae. 12. *A. gnom*, ventral femoral patch. 13. *A. ampla*, tergal posterior margin. 14. *A. gnom*, tergal posterior margin. 15. *A. turbida*, tergal posterior margin. 16. *A. turbida*, sternal friction pad. (Scale: Figs. 12–16—bar = 10 μ m; Fig. 14—no bar)

49e) of all legs with long setae minutely, multilaterally ciliate (the ciliae are relatively short and sparse) or with short glabrate bristles dorsally (*ibid.*: fig. 46e); ventral femoral patch present (Figs. 1, 12). Metatibia with one row of bristles dorsally. Tarsus of all legs without long, ventral subapical seta. Claws with one row of denticles.

Abdomen without dorsal tubercles; often dorsoventrally flattened. Tergal scales and scale bases absent (Figs. 13, 14); median row of long hyaline bristles present or absent dorsally; tube scales present (as in Fig. 8) or absent. Posterior marginal spines (Figs. 13–15) poorly developed, often spiculate or multidentate. Gills simple and

without serrate margins. Cerci with lateral bristles. Median terminal filament generally reduced.

Adult. Forewings with paired marginal intercalaries; crossveins and adjoining membranes unpigmented. Hindwings present or reduced and without costal process, or hindwings absent. Metascutellum flattened and directed posterad (Edmunds et al., 1976: fig. 261). Male genitalia often with strongly sclerotized and rectangulate process (Müller-Liebenau, 1970: fig. 42a, b; Traver, 1935: fig. 168) present between forceps bases.

Type species. Acentrella lapponica Bengtsson 1912:110, by original designation.

Material examined. *Acentrella lapponica* Bengtsson: 1 larva, Lappland, Sitojoure ö skemmia, örre bjöskrogious, 10.vii.1960, Lok. m. 18, leg. Brink (ZSM); 1 larva, Lappland; 1 larva, Alaska, South Slope, Yukon River System, 29.vii.1972 (USNM); 1 larva, Canada, Northwest Territories, Lake Harbour, Baffin Island, 5.vii.1935 (PERC); 1 larva, Alaska, Atigua River, 1971 (PERC). *Acentrella sinaica* Bogoescu, 1 larva, Portugal, 1971, leg. Puthz (ZSM). *Pseudocloeon gnom* Kluge, 5 larvae, Japan, Yoshino River, Kamiichi Bridge, 18.viii.1984, N. Kobayashi (PERC). *Pseudocloeon turbidum* McDunnough (tentative larval association—RDW), 12 larvae, Oregon, Lane County, Wildcat Creek, 16.v.1982, leg. G.W. Courtney (OrSU). Numerous collections of Nearctic *Baetis amplus* (Traver), *Baetis insignificans* McDunnough, and *Pseudocloeon carolina* (Banks) (BK, CU, PERC, SWRC, USNM, UU, VPI).

Included species. Nominal species that we can presently assign to *Acentrella* are *A. lapponica* Bengtsson, 1912 (type species); *A. ampla* Traver, 1932; *A. carolina* (Banks), 1924, **New Combination** (previously Nearctic *Pseudocloeon*); *A. chantauensis* (Kluge), 1981, **New Combination** (previously Palearctic *Baetis*); *A. fenestrata* (Kazlauskas), 1963 **New Combination** (previously Palearctic *Pseudocloeon*); *A. gnom* (Kluge), 1983, **New Combination** (previously Palearctic and Oriental *Pseudocloeon*) [= *Pseudocloeon ultimum* Müller-Liebenau, 1985, **New Synonymy**]; *A. insignificans* (McDunnough), 1926, **New Combination** (previously Nearctic *Baetis*); *A. lata* (Müller-Liebenau), 1985, **New Combination** (previously Palearctic *Pseudocloeon*); *A. sibirica* (Kazlauskas), 1963, **New Combination** (previously Palearctic *Pseudocloeon*); *A. sinaica* Bogoescu, 1931; *A. tonneri* (Braasch and Soldán), 1983, **New Combination** (previously Palearctic *Baetiella*) and *A. turbida* (McDunnough) 1924, **New Combination** (previously Nearctic *Pseudocloeon*). We regard *Acentrella suzukiella* Matsuura (1931) as provisionally assignable to *Acentrella* on the basis of published descriptions. The Afrotropical species *A. capensis* Barnard (1932), *A. monticola* Crass (1947), *A. natalensis* Crass (1947), and *A. sp.* A Kimmins (1955) are not congeneric with *Acentrella* but cannot be formally reclassified until a comprehensive review of these species is possible.

Distribution. Holarctic and Oriental.

Remarks. As redefined herein larvae of the genus *Acentrella* Bengtsson may be separated from all other *Baetis* complex genera by the following combined characters: compact labium with reduced and apically rounded to truncate labial palps; femora, and often the tibia, with relatively long (compared to other *Baetis* species) dorsal bristles; only one row of metatibial bristles; absence of a long distal tibial bristle; absence of tergal scales; poorly developed posterior marginal spines of the abdominal terga; and cerci with prominent lateral setae.

Acentrella includes species with hindwings, species with reduced hindwings, and

species without hindwings. The previous diagnoses (Müller-Liebenau, 1981, 1985) of this genus, which were based on reduced size and sexually dimorphic character states of the adult hindwing, are untenable on the basis of larval characters described herein.

Based on outgroup (Holarctic *Baetis*) comparisons, the genus *Acentrella* appears to have been derived from a *Baetis*-like ancestor that as larvae possessed short, glabrous dorsal femoral and tibial bristles, well-developed hindwing pads, scaled abdominal terga, well-developed posterior marginal spines, spinous margined gills, and a median terminal filament subequal to the cerci. From this a derived lineage constituting *Acentrella* demonstrates the following apomorphies in its most ancestral species: 1) compaction of the mouthparts including a reduction in the relative lengths of the labial palp segments, 2) reduction of the hindwing pads, 3) loss of abdominal tergal scales, 4) reduction of the posterior marginal spines, 5) loss of marginal spines on the gills, and 6) reduction in the size of the median terminal filament relative to the cerci.

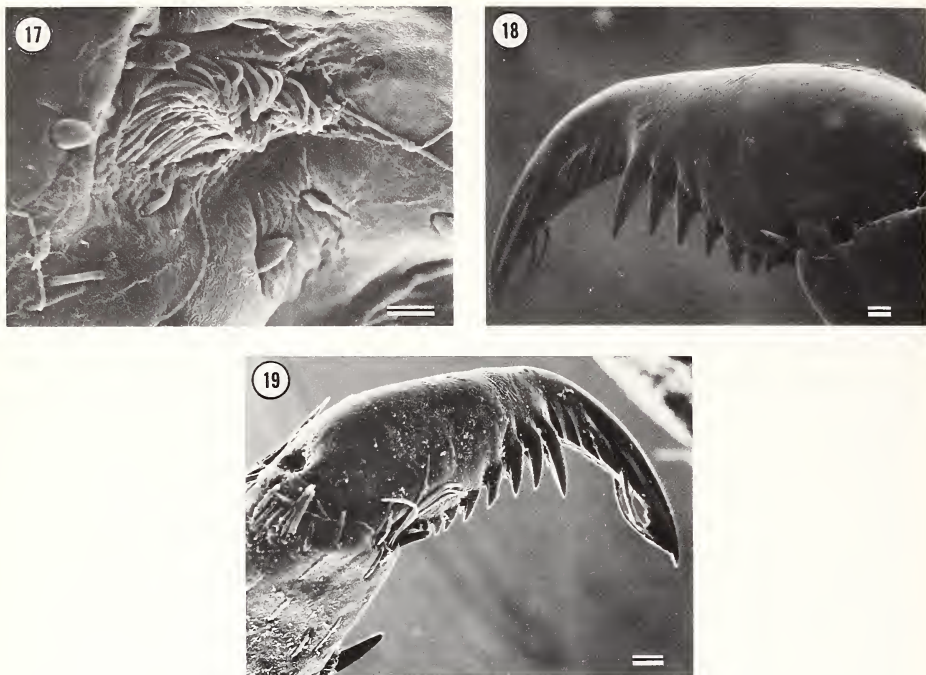
Genera closely allied to *Acentrella* include *Heterocloeon* McDunnough (Moriyama and McCafferty, 1979c) and *Liebebiella*. Species previously associated with *Pseudocloeon* that were found to be closely allied to *Heterocloeon* by Moriyama and McCafferty (1979c) belong to *Acentrella*.

Within *Acentrella* several apomorphic larval characters appear that may be indicative of phylogenetically related subgroups of species within the genus. One such character is the presence of spiculate or multidentate posterior marginal spines (Fig. 15) of the abdominal terga. Although all species of *Acentrella* possess reduced posterior marginal spines, some species, e.g., *A. lapponica*, *A. carolina*, *A. chantauensis*, *A. fenestrata*, *A. sibirica*, *A. sinaica*, and *A. turbida*, possess posterior marginal spines that are very reduced and that form distinct spiculae, some or all of which may be multidentate depending on the species considered. The relatively more ancestral posterior marginal spines found in the remaining species of *Acentrella* retain the appearance of a single row of distinctly formed spines that are not spiculate (Fig. 13). The subgroup including *A. lapponica* also shows a tendency for a dorsoventral flattening of the abdomen and a correlated increase in the size of the paired abdominal friction pads (Fig. 16) that individually may extend to cover about one-third of each abdominal sternite, and a tendency for dark-colored abdominal terga 2-6 in the adult stage rather than light colored terga as may be found in other species.

In the majority of *Acentrella* species we examined, the clypeus and labrum are distinctly folded beneath the head capsule as described and illustrated by Edmunds et al. (1976: fig. 111), although at least one of the relatively more enigmatic species, *A. ampla*, does not possess this character. We have seen baetids including members of the Nearctic *Baetis propinquus* species group (Moriyama and McCafferty, 1979b) and other species, which are clearly unrelated to *Acentrella* and its cognates, that have independently derived a similar positioning of the clypeus and labrum beneath the head capsule.

Baetiella Ueno, 1931

Neobaetiella Müller-Liebenau, 1985:103, **New Synonymy**. [Type species. *Neobaetiella uenoi* Müller-Liebenau, 1985:108, by original designation.]



Figs. 17–19. *Baetiella* spp. larvae. 17. *B. japonica*, ventral femoral patch. 18. *B. japonica*, claw. 19. *B. bispinosa*, claw. (Scale: Figs. 17–19—bar = 10 μ m)

The genus *Baetiella* Ueno has been variously regarded as a subgenus of *Pseudocloeon* Klapálek (Kazlauskas, 1963) or a synonym of *Pseudocloeon* (Bogoescu and Tabacaru, 1957; Gose, 1980; Müller-Liebenau, 1985). We regard *Baetiella* as a distinct and valid genus.

Description. Larva. Antennae ca. $1.5\times$ length of head capsule. Mandibular incisors (Müller-Liebenau, 1985: fig. 6e) discernible one from another, i.e., with visible fusion line. Maxillary palp two segmented (*ibid.*: fig. 6d). Labium (Fig. 3; *ibid.*: fig. 6b) with palps shortened; segment 2 of palp with weakly developed inner lobe; segment 3 of palp distinctly coniform and symmetric.

Prothorax without distinctive *lapponica*-type color pattern. Femora of all legs with long, non-ciliate bristles (*ibid.*: fig. 6m); ventral femoral patch present (Figs. 1, 17). Metatibia with one row of long dorsal bristles. Tarsus of all legs without long ventral subapical bristle. Claws (Figs. 18, 19) with one row of denticles.

Abdomen with single or paired dorsal tubercles (Fig. 20; *ibid.*: fig. 13; Gose, 1980: fig. 53) or without dorsal tubercles and not dorsoventrally flattened. Scales present or absent, median row of long, hyaline bristles absent dorsally; tube scales sometimes present. Posterior marginal spines (Fig. 21) numerous, distinct, and entire. Gills simple and without serrate margins. Cerci with numerous bristles or with numerically reduced lateral bristles (Figs. 22, 23) on interior margin. Median terminal filament shorter than cerci.

Adult. Forewings (Gose 1965: fig. 1) with paired marginal intercalaries and often

with distinctly pigmented areas adjoining and including the crossveins. Metascutellum (Edmunds et al., 1976: fig. 262) not flattened but projecting dorsoposteriorly. Male genitalia without medial process (Gose, 1965: fig. 4).

Type species. Acentrella japonica Imanishi, 1930:110, by original designation (Ueno, 1931).

Material examined. Baetiella japonica (Imanishi), 2 male imagos, Japan, Sagami River, Ogra Bridge, 29.xi.1984, leg. N. Kobayashi (PERC); 5 larvae, Japan, Kawazu River, Kawazu Bridge, 4.iii.1985, leg. N. Kobayashi (PERC); 30 larvae, Korea, Taeha, Ullung, Kyongsanbuk-do, 3.viii.1983, leg. Y. J. Bae (PERC); 5 larvae, Korea, Taebaeksan, Taebaek, Kangwon-do, 13.viii.1983, leg. Y. J. Bae (PERC). *Pseudocloeon bispinosa* Gose, 15 larvae; Taiwan; Tahan River near Wu-Liao (about 23 km SW Taipei), 9.x.1978, G. F. and C. H. Edmunds (UU). *Baetiella ladakae* Traver, paratype male imago, forewing (slidemounted) and male genitalia (slidemounted) (UU). *Pseudocloeon tuberculatum* Kazlauskas, 6 larvae, Korea, Chojongchon, Kapyong, Kyonggi-do, 26.iv.1973, leg. I. B. Yoon (PERC). *Baetiella* sp. male imago, Rokki, Formosa (Taiwan), 13.vi.1932, leg. J. L. Gressitt (MCZ). *Baetiella* sp., Traver, 1939, 1 larva, Kashmir, Kangan, Sind River, collection K-57, 16.v.1932, alt. 5,795 ft. (UU).

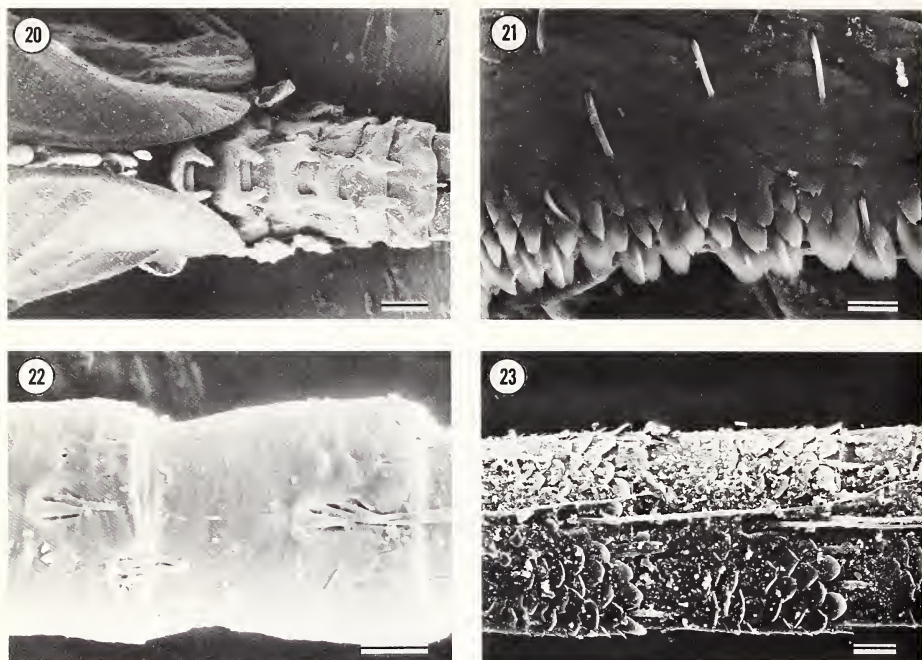
Included species. Baetiella japonica (Imanishi), 1930 (type species); *Baetiella aino* (Matsumura), 1931, **New Combination** (previously Palearctic *Pseudocloeon*); *B. armata* Braasch; *B. ausobskyi* Braasch; *B. bispinosa* (Gose), 1980, **New Combination** (previously Palearctic *Pseudocloeon*) [= *Neobaetiella macani* Müller-Liebenau, 1985:108, **New Synonymy**] [= *Neobaetiella imanishi* Müller-Liebenau, 1985:108, fig. 19, **Nomen Nudum** (an editorial oversight)]; *B. imanishii* Braasch; *B. innotata* (Braasch), 1978, **New Combination** (previously Palearctic *Baetis*); *B. ladakae* Traver, 1939; *B. marginata* Braasch; *B. muchei* (Braasch), 1978, **New Combination** (previously Palearctic *Pseudocloeon*); *B. tuberculata* (Kazlauskas), 1963, **New Combination** (previously Palearctic *Pseudocloeon*) [= *Neobaetiella uenoi* Müller-Liebenau (1985:107), unavailable name, Articles 1b(6) and 13b ICZN]; and *B. ursina* (Kazlauskas), 1963, **New Combination** (previously Palearctic *Baetis*).

Distribution. Palearctic, Oriental.

Remarks. Larvae of *Baetiella* are distinct from all other *Baetis* complex genera by the uniquely conical form of the third labial palpal segment; femora with relatively long (compared to other *Baetis* complex species) dorsal bristles; numerous and distinct posterior marginal spines; and an abdomen that is not dorsoventrally flattened.

Although we do not know the general applicability of Kluge's (1983) biological and behavioral observations regarding *B. tuberculata*, we do emphasize two points that may eventually be found to have systematic significance. First, is an observation that the subimago of *B. tuberculata* rests with its wings outstretched. Other baetid subimagos that we know of hold the wings vertically uplifted over the body. The second observation is that the pigmentation of the forewings takes approximately 24–48 hours to develop fully. This latter observation has obvious implications in that preserved specimens of teneral adults (less than 24 hr old) may not possess the characteristic pigmentation of the wings.

Baetiella appears to have been derived independently of *Acentrella*. This conclusion is supported by numerous character data. We hypothesize that *Baetiella* was derived from a *Baetis*-like ancestor, but the particular species complex for outgroup comparisons of *Baetiella* is not clear. Müller-Liebenau (1970) suggested that *B. ursina*,



Figs. 20–23. *Baetiella* spp. larvae. 20. *B. bispinosa*, dorsal abdomen. 21. *B. japonica*, tergal posterior margin. 22. *B. tuberculata*, cerci. 23. *B. bispinosa*, cerci. (Scale: Fig. 20—bar = 100 μ m; Figs. 21–23—bar = 10 μ m)

which we regard as a relatively plesiomorphic species of *Baetiella*, appeared to be related to the *Baetis niger* group of species. Our own review of this species, based in part on adult data presented by Kluge (1983), indicates a possible relationship with *Baetis lutheri* Müller-Liebenau due to similarities of the male genitalia and striking similarities in the larval mouthpart and tergal structures. The synapomorphies defining *Baetiella*, i.e., the uniquely formed mouthparts, tergal armature, gills, reduced median terminal filament and characters of the cerci, are evidently derived from within the *Baetis* complex of genera and independent of the *Acentrella* lineage.

The relatively most ancestral species of *Baetiella* are the distinctive and possibly synonymous Palearctic *B. ursina* and *B. innotata*. These retain a moderately developed median terminal filament, cerci that bear numerous bristles along the interior margin and that are shorter than the body in length, tergal scales, and a well-developed hindwing pad in the larval stage. In all other known *Baetiella* the median terminal filament of the larval stage is reduced to one segment, the cerci bear numerically reduced bristles along the interior margin and are of variable length but often longer than the body in length, tergal scales are absent, and the hindwing pad is greatly reduced or absent. Kluge (1983) has described the adult of *B. ursina*, which apparently differs from other known *Baetiella* species by the retention of the relatively plesiomorphic condition (determined by outgroup comparisons, i.e., *Baetis*) of forewings

that are clear and unpigmented. Other known adults of *Baetiella* possess clearly pigmented areas adjacent to and including the crossveins of the forewings.

Baetiella japonica na Imanishi and *Baetiella japonica* (Imanishi), the type species, are not the same. The type species of *Neobaetiella* was improperly designated by Müller-Liebenau (1985) to be the descriptively proposed and temporary taxon *Baetiella japonica na* Imanishi, 1940, for which she proposed the new name *Neobaetiella uenoi* Müller-Liebenau (1985:107) (erroneously cited as new combination). The designation of a new name for the above taxon does not meet the criteria of name availability [International Code of Zoological Nomenclature, 3rd ed., Article 1, b(6) and Article 13] because the description of *Baetiella japonica na* by Imanishi was clearly intended as a temporary reference [Article 1, b(6)] and not a formally described taxon. Furthermore, Kluge (1983) demonstrated that the proper name to which Imanishi's (1940) larva refers was *Pseudocloeon tuberculatum* Kazlauskas, 1963 (now *Baetiella tuberculata*). In addition, *Baetiella noseawensis* Gose, 1965, was designated a junior synonym of *P. tuberculatum* by Kluge (1983). Müller-Liebenau (1985) included discussions of *P. tuberculatum* in her review, but did not formally transfer it to *Neobaetiella* (1985:108). In any case, her intended type of *Neobaetiella* is actually synonymous with *B. tuberculata*.

Based on our study of *B. tuberculata*, we found that in all characters (both larval and adult) this species is not generically distinct from other *Baetiella* and is congeneric with *B. japonica* (the type species of *Baetiella*). *Baetiella tuberculata*, *B. ausobskyi*, *B. armata*, and *B. imanishii* are uniquely characterized among all other described *Baetiella* by the presence of a dorsal tubercle on the posterior margin of the abdominal terga. *Baetiella bispinosa* [the only other nominal species originally placed in *Neobaetiella* as *N. macani* by Müller-Liebenau (1985)] possesses bilobed tubercles on the posteriormost abdominal terga and a single tubercle on segments 1–3. The presence and condition, or absence, of tubercles is intragenerically variable in at least some other baetid genera, e.g., *Jubabaetis* (unpublished) and the New World genus *Baetodes* (Cohen and Allen, 1978). Further, the distinctive and highly derived *B. bispinosa* possesses all of the synapomorphic characters that we regard as diagnostic for larvae of the genus *Baetiella*.

ACKNOWLEDGMENTS

We thank N. H. Anderson, Oregon State University (OrSU), Corvallis; Yeon Jae Bae, Korea University, Seoul; G. F. Edmunds, Jr., University of Utah (UU), Salt Lake City; O. S. Flint, Jr., National Museum of Natural History (USNM), Washington; Norio Kobayashi, Ota-ku, Tokyo; I. Müller-Liebenau, Max Planck Institut für Limnologie, Plön [material deposited in the Zoologisches Staatsmuseum, Munich (ZSM)]; H. Strümpel, Zoologisches Institut und Zoologisches Museum, Hamburg; and Charles Vogt, Harvard Museum of Comparative Zoology (MCZ), Cambridge, for the loan of materials. We thank Norio Kobayashi and Kyuemon Gose, Gojo City, Japan, for reprints of various papers on Japanese mayflies. We also thank D. Bloodgood and A. V. Provonsha for assistance with SEM photographs. Research funding was in part provided by National Science Foundation grant NSF PCM-8400133 to the Purdue University Electron Microscopy Center in Agriculture. This paper has been assigned Purdue University Exp. Sta. Journal Number 10,728.

LITERATURE CITED

Banks, N. 1924. Descriptions of new neuropteroid insects. Bull. Harv. Univ. Mus. Comp. Zool. 65:421–455.

- Barnard, K. H. 1932. South African mayflies (Ephemeroptera). Trans. R. Soc. South Africa, Cape Town 20:201-259.
- Bengtsson, S. 1912. Neue Ephemeriden aus Schweden. Entomol. Tidskr. 33:107-117.
- Bogoescu, C. 1931. Une nouvelle espèce d'*Acentrella* Bgtss. (Ephéméroptère) *Acentrella sinaica* n. sp. Boll. Sect. Sci. Acad. Roumaine 14:197-202.
- Bogoescu, C. and I. Tabacaru. 1957. Etude comparée des nymphes d'*Acentrella* et de *Pseudocloeon*, considérations phylogénétiques concernant la famille Baetidae (Ephemeroptera). Beitr. z. Entomol. 7:483-492.
- Braasch, D. 1978. Baetidae (Ephemeroptera) in Mittelasien I. Entomol. Nachr. 22:17-23.
- Braasch, D. 1983. Neue Baetidae von Nepal (Ephemeroptera). Reichenbachia 21:147-155.
- Braasch, D. and T. Soldán. 1983. Baetidae in Mittelasien III (Ephemeroptera). Entomol. Nachr. Berich. 27:266-271.
- Cohen, S. D. and R. K. Allen. 1978. Generic revisions of mayfly nymphs III. *Baetodes* in North and Central America (Baetidae). J. Kansas Entomol. Soc. 51:253-269.
- Crass, R. S. 1947. The may-flies (Ephemeroptera) of Natal and the Eastern Cape. Ann. Natal Mus. 11:37-110.
- Demoulin, G. 1970. Ephemeroptera des faunes éthiopienne et malgache. South African Animal Life, results of the Lund University Expedition in 1950-1951. 14:24-170.
- Edmunds, G. F., Jr. 1974. Some taxonomic changes in Baetidae (Ephemeroptera). Proc. Entomol. Soc. Washington 76:289.
- Edmunds, G. F., Jr., S. Jensen and L. Berner. 1976. Mayflies of North and Central America. Univ. Minnesota Press, Minneapolis.
- Edmunds, G. F., Jr. and J. R. Traver. 1954. An outline of reclassification of the Ephemeroptera. Proc. Entomol. Soc. Washington 56:236-240.
- Gillies, M. T. 1979. *Cloeon pusillum* Navás, a species of *Afrobaetodes* Demoulin. Entomol. Mon. Mag. 114:153-154.
- Gose, K. 1965. Description of two new species of Baetidae from Japan (Ephemeroptera). Kontyu 33:218-220.
- Gose, K. 1980. The mayflies of Japan. Key to the families, genera, and species. Part 7. Kaiyou to Seibutsu 2(3):211-215.
- Grandi, M. 1956. Contributi allo studio dell'Ephemeropteri italiani. XXI. Intorno ai generi *Acentrella* Bgtssn. e *Baetis* Leach. Boll. Inst. Entomol. Univ. Bologna, pp. 119-124.
- Grandi, M. 1960. Ephemeroptera. Fauna d'Italia, Volume 3, Italian National Academy, Department of Entomology and Italian Union of Zoology, Bologna.
- Imanishi, K. 1930. Mayflies from Japanese torrents I. New mayflies of the genera *Acentrella* and *Ameletus*. Trans. Nat. Hist. Soc. Formosa 20:263-267.
- Imanishi, K. 1940. Ephemeroptera of Manchoukuo, inner Mongolia, and Chosen. Report of the Limnobiological Survey of Kwantung and Manchoukuo, pp. 169-263.
- Kazlauskas, R. 1963. New and little known mayflies from the USSR. Entomol. Rev. 42:582-593.
- Keffermüller, M. 1980. Un changement dans la taxonomie de la famille Baetidae. Pages 115-121 in: J. F. Flannagan and K. E. Marshall (eds.), Advances in Ephemeroptera Biology. Plenum Publishing Corporation, New York.
- Kimmins, D. E. 1955. Ephemeroptera from Nyasaland, with descriptions of three new species and some interesting nymphal forms. Ann. Mag. Nat. Hist., Ser. 12 8:859-880.
- Klapálek, F. 1905. Plecopteren und Ephemeropteren aus Java, gesammelt von Prof. K. Kraepelin 1904. Mitt. Hamburg. Nat. Hist. Mus. 22:101-107.
- Kluge, N. Yu. 1981. A new species of the genus *Baetis* (Ephemeroptera, Baetidae) from Kazakhstan. Acad. Sci., USSR, 9:1418-1419.
- Kluge, N. Yu. 1983. New and little known mayflies of the fam. Baetidae (Ephemeroptera) from the Primor'ye. Entomol. Rev. 62:53-68.
- Matsumura, S. 1931. Ephemeroptera. In: S. Matsumura (ed.), 6000 Illustrated Insects of Japan-Empire. Tokyo.

- McDunnough, J. 1924. New Canadian Ephemeroidea with notes, II. *Can. Entomol.* 56:90–98, 113–122.
- McDunnough, J. 1926. Notes on North American Ephemeroidea with descriptions of new species. *Can. Entomol.* 58:184–196.
- Morihara, D. K. and W. P. McCafferty. 1979a. The *Baetis* larvae of North America. *Trans. Am. Entomol. Soc.* 105:139–221.
- Morihara, D. K. and W. P. McCafferty. 1979b. Systematics of the *propinquus* group of *Baetis* species (Ephemeroidea: Baetidae). *Ann. Entomol. Soc. Am.* 72:130–135.
- Morihara, D. K. and W. P. McCafferty. 1979c. The evolution of *Heterocloeon* with the first larval description of *Heterocloeon frivulus* comb. n. (Ephemeroidea: Baetidae). *Aq. Insects* 1:225–231.
- Müller-Liebenau, I. 1965. Revision der Simon Bengtsson aufgestellten *Baetis*-Arten. *Opusc. Entomol.* 30:79–123.
- Müller-Liebenau, I. 1970. Revision der europäischen Arten der Gattung *Baetis* Leach, 1815 (Insecta, Ephemeroidea). *Gewässer und Abwässer* 28/29(1969):1–214.
- Müller-Liebenau, I. 1973a. Morphological characters used in revising the European species of the genus *Baetis* Leach. *Proc. First Int. Conf. Ephemeroidea* 1970:182–198.
- Müller-Liebenau, I. 1978. *Raptoabaetopus*, eine neue carnivore Ephemeroidea-Gattung aus Malaysia (Insecta, Ephemeroidea: Baetidae). *Arch. f. Hydrobiol.* 82:465–481.
- Müller-Liebenau, I. 1980. Ergänzungen zur Beschreibung von *Raptoabaetopus orientalis* Müller-Liebenau, 1978 (Insecta, Ephemeroidea). *Arch. f. Hydrobiol.* 88:388–390.
- Müller-Liebenau, I. 1981. Review of the original material of the baetid genera *Baetis* and *Pseudocloeon* from the Sunda Islands and the Philippines described by G. Ulmer, with some general remarks (Insecta: Ephemeroidea). *Mitt. Hamburg Zool. Mus. Inst.* 78:197–208.
- Müller-Liebenau, I. 1982a. New species of the family Baetidae from the Philippines (Insecta, Ephemeroidea). *Arch. f. Hydrobiol.* 94:70–82.
- Müller-Liebenau, I. 1982b. Five new species of *Pseudocloeon* Klapálek, 1905 (Fam. Baetidae) from the Oriental region (Insecta, Ephemeroidea) with some general remarks on *Pseudocloeon*. *Arch. f. Hydrobiol.* 95:282–298.
- Müller-Liebenau, I. 1984a. New genera and species of the family Baetidae from West-Malaysia (River Gombak) (Insecta: Ephemeroidea). *Spixiana* 7:253–284.
- Müller-Liebenau, I. 1984b. Baetidae from Sabah (East Malaysia) (Ephemeroidea). *Proc. Fourth Int. Conf. Ephemeroidea*, pp. 85–99.
- Müller-Liebenau, I. 1985. Baetidae from Taiwan with remarks on *Baetiella* Ueno, 1931 (Insecta, Ephemeroidea). *Arch. f. Hydrobiol.* 104:93–110.
- Müller-Liebenau, I. and M. D. Hubbard. 1986. Baetidae from Sri Lanka with some general remarks on the Baetidae of the Oriental Region (Insecta: Ephemeroidea). *Florida Entomol.* 68:537–561 (1985).
- Traver, J. R. 1932. Mayflies of North Carolina. *J. Elish. Mitch. Sci. Soc.* 47:85–161, 163–236.
- Traver, J. R. 1935. Part II, Systematic. Pages 239–739 in: J. G. Needham et al. (eds.), *The Biology of Mayflies*. Comstock Publ. Co., Ithaca, New York.
- Traver, J. R. 1939. Himalayan mayflies (Ephemeroidea). *Ann. Mag. Nat. Hist., Ser. 11*, 4: 49–56.
- Ueno, M. 1931. Contributions to the knowledge of Japanese Ephemeroidea. *Annotat. Zool. Japonenses* 13:189–226.
- Ulmer, G. 1939. Eintagsfliegen (Ephemeroidea) von den Sunda Inseln. *Arch. f. Hydrobiol., Suppl.* 16:443–692.
- Waltz, R. D. and W. P. McCafferty. 1985a. Redescription and new lectotype designation for the type species of *Pseudocloeon*, *P. kraepelini* Klapálek (Ephemeroidea: Baetidae). *Proc. Entomol. Soc. Washington* 87:800–804.

- Waltz, R. D. and W. P. McCafferty. 1985b. Illustration and lectotype designation for *Baetis feminalis* Eaton (Ephemeroptera: Baetidae). *Orient. Insects* 18:335-337.
- Waltz, R. D. and W. P. McCafferty. 1985c. A new species of *Procloeon* from Taiwan (Ephemeroptera: Baetidae). *Orient. Insects* 19:121-123.
- Waltz, R. D. and W. P. McCafferty. 1986. *Apobaetis etowah*, a new combination in Nearctic Baetidae (Ephemeroptera). *Proc. Entomol. Soc. Washington* 88:191.
- Waltz, R. D. and W. P. McCafferty. 1987a. New genera of Baetidae for some Nearctic species previously included in *Baetis* Leach (Ephemeroptera). *Ann. Entomol. Soc. Am.* (in press).
- Waltz, R. D. and W. P. McCafferty. 1987b. Revision of *Cloeodes* Traver (Ephemeroptera: Baetidae). *Ann. Entomol. Soc. Am.* 80:191-207.
- Waltz, R. D. and W. P. McCafferty. 1987c. New genera of Baetidae (Ephemeroptera) from Africa. *Proc. Entomol. Soc. Washington* 89:95-99.
- Waltz, R. D. and W. P. McCafferty. 1987d. A generic revision of *Cloeodes* Traver and description of two new genera (Ephemeroptera: Baetidae). *Proc. Entomol. Soc. Washington* 89:177-184.

Received January 28, 1987; accepted April 6, 1987.